

27. The Chondrocranium of the Teleostean Fish *Sebastes marinus*. By N. A. MACKINTOSH, B.Sc., Demonstrator in Zoology, Imperial College of Science, South Kensington.*

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1. INTRODUCTION.

The work of Parker and subsequently that of Gaupp, Böker, and others, on the skull of *Salmo*, constitutes the basis of our knowledge of the cranial development of the Teleostomi. Further contributions have been made by Stöhr, McMurrich, Allis, Winslow, Swinnerton, and Pehrson amongst others. In 1910 Allis published a paper dealing in some detail with the cranial anatomy of the mail-checked fishes. This paper dealt with the osteology, and to some extent the latero-sensory canals and muscles of the adult cranium, but, so far as I am aware, no work has so far been done on the development of the cartilaginous skull of any of the Scorpenidae. It is hoped that the present paper will take a step towards meeting this deficiency in that it describes the chondrocranium of a fairly representative member of the group.

The following description is not an exhaustive comparative account, and few generalizations will be made; it deals with the development of the chondrocranium from a very early stage up to the time when the cartilaginous elements of the head are fully developed. Certain comparisons with other forms will be made where points of special interest or peculiarity arise.

The work was undertaken at the suggestion of Prof. MacBride and I wish to take the opportunity of thanking him and Mr. H. G. Cannon for many helpful suggestions.

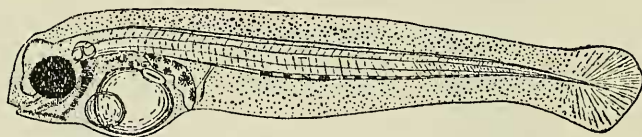
* Communicated by Prof. E. W. MACBRIDE, F.R.S., F.Z.S.

2. MATERIAL AND METHOD.

Some difficulty in obtaining all the desirable material has rendered the series of developmental stages a little incomplete, for I was unable to procure any specimens between the 5.5 mm. and 25 mm. stages. This leaves rather a large gap during which a considerable development of cartilage takes place. It is not difficult, however, to reconstruct the more important processes which occur during this period.

I had at my disposal large quantities of specimens from the early segmentation stages up to the 5.5 mm. stage, and three or four specimens ranging between 25 and 30 mms. The abundance early stages compensates to some extent for the lack of some of the later stages.

Text-figure 1.



Stage 3. External features.

It has been found most convenient to divide the following account into four parts:—

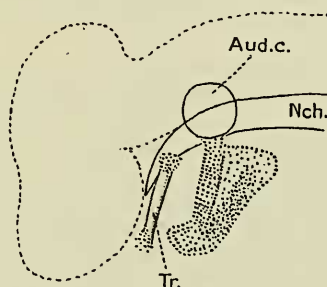
- Stagel. The unhatched embryo.
- „ 2. The 4.5 mm. larva.
- „ 3. The 5.5 mm. larva.
- „ 4. The 25 mm. post-larval stage.

Stages 2 and 3 are close together, but the differences between them are sufficient to justify their separate consideration. The specimens for stages 1–3 were supplied from Lowestoft and those for the 25 mm. stage were supplied by the Board of Fisheries for Scotland at Aberdeen. Fixation was in every case in formalin. Consequently it was not easy to follow much of the histological details of the formation of cartilage, though preservation was otherwise satisfactory. The principal stains used were thionin and orange G, Mallory's triple stain and picronigrosin. For the first stage specimens were removed from the egg capsule for sectioning. The diameter of the curled up embryo is at this stage about 1 mm. The eyes can already be seen with the naked eye and serve as a useful guide for orientation. The 4.5 mm. larva has just escaped from the egg capsule and still retains a large yolk sac. In most respects it closely resembles the 5.5 mm. larva. In the latter (text-fig. 1) the yolk sac is considerably reduced though it is still a fairly substantial body. The principal features of this larva are the very long tail, the large eyes, and the distinct cranial flexure. The mouth is still in a more or less ventral

position, but has shifted further forward than in the 4.5 mm. stage. The auditory vesicles are fairly well advanced and can be seen clearly in whole mounts. Large pigment cells are to be seen over the posterior part of the gut, and there is a row along the ventral side of the tail. The 25 mm. specimens are of a post-larval stage and exhibit roughly the form of the adult.

Reconstructions were in each case made from series of transverse sections cut at 10 μ . These were examined with the aid of a squared eyepiece micrometer, and lateral and dorsal views were plotted directly on to squared paper. The details of this method are described in a recent paper by Wells (1922) on the chondrocranium of *Chupea*. As it is necessary in this method to have a

Text-figure 2.



Stage 1. Lateral view of chondrocranium.

base line from which all measurements are made it is usual to assume that some element in the head, generally the notochord or some piece of cartilage, is straight. I have been able to avoid this assumption by plotting an accurate outline of the head before sectioning it, and then taking all measurements from the outline. Other methods of reconstruction are described by Norman (1923) in a paper dealing specially with the subject.

3. THE CHONDROCRANIUM

a. Stage 1. *The unhatched embryo.*

This is the earliest stage it was found profitable to investigate (text-fig. 2). The head skeleton is in an extremely elementary condition, and is represented principally by tracts of procartilage and connective-tissue cells which are becoming concentrated into the positions in which cartilage is subsequently to be laid down. It is always a matter of some difficulty to draw a definite line between procartilage and cartilage proper. The trabeculae at this stage appear to be in an intermediate condition. The outline is quite definite, but the cells have not become thoroughly welded together to form a solid matrix. The trabeculae are very short

paired rods, ending freely at both ends and lying just below the apex of the notochord and behind the forebrain. There is a marked cranial flexure. At present there is no sign of the parachordals.

The visceral skeleton is represented by a relatively extensive but barely differentiated mass of procartilage. In this it is possible to distinguish on each side an element running downwards from the auditory vesicle. This element ultimately gives rise to the jaw suspension apparatus. At the foot of it the procartilage runs forwards for a short distance indicating the position in which Meckel's cartilage is to be laid down. This cartilage appears later as a condensation on each side which grows forwards as the cranial flexure is eased and the mouth moves forwards. At the present stage the mouth has not appeared. The rest of the mass of procartilage extends upwards and backwards and constitutes the rudiments of the branchial bars.

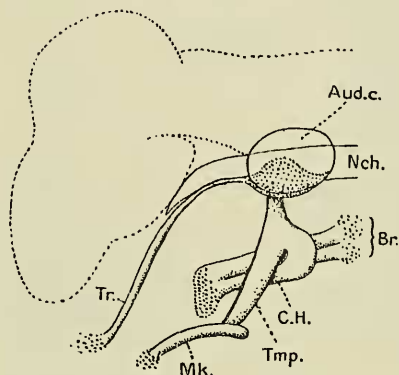
b. Stage 2. *The 4.5 mm. larva.*

The trabeculae have at this stage lengthened considerably (text-fig. 3) and form a roof to the mouth, which has now made its appearance. The parachordals are now established and are continuous with the trabeculae, but where they form the floor of the auditory capsule they are in a procartilaginous condition. They cannot, however, be distinguished as anterior and posterior plates as in the case of *Salmo*, *Gasterosteus*, etc. The trabeculae are closely approximated along the whole of their length and end freely anteriorly, though there is at their extremity a condensation of connective tissue representing the ethmoid plate. The notochord reaches well forward and turns down under the rudiment of the infundibulum.

In the visceral skeleton Meckel's cartilage has made its appearance, its two components being joined anteriorly by a tract of procartilage. A substantial bar of cartilage articulates with the lower jaw near its posterior end and with the lower surface of the auditory capsule. This element, which appears to be a piece of continuous cartilage, later gives rise to the hyomandibular, symplectic, and quadrate cartilages. Pouchet (1878) employed the term "primordial temporal" to a somewhat similar element which he found in certain forms. As "temporal" is now obsolete as an alternative name for the hyomandibular, and as I am unaware of any name at present in use which could rightly be applied to the bar which, in *Sebastes*, joins the lower jaw to the auditory capsule, I propose for convenience to call it the temporal cartilage. From the posterior side of this temporal cartilage a branch is given off which turns inwards and forwards as the ceratohyal to join the anterior end of a mass of cartilage from which the branchial bars are beginning to be differentiated. The point at which the ceratohyal branches off is composed of rather immature cartilage which later becomes more compact and forms the stylohyal.

A remarkable feature which has become evident at this stage is the precocious development of the visceral skeleton. The lower jaw, temporal, ceratohyal, and to some extent the first two branchial bars are all distinguishable, while the cranium consists only of the simple parallel trabeculae and the barely established parachordals. It is interesting at this point to note in connection with the form assumed by the parachordals that Filatoff (1916) has shown that if the auditory vesicle of *Bufo* is transplanted to a position overlying the trabeculae a cartilaginous capsule tends to

Text-figure 3.



Stage 2. Lateral view of chondrocranium.

form round it, while the parachordals from which the vesicle has been removed do not form a capsule. It is pointed out that the formation of the cartilaginous capsule is not an inherent property of the parachordals, but depends upon the presence of the vesicle.

From now onwards the mouth tends to move forwards and upwards, and Meckel's cartilage follows it by growth at the anterior end.

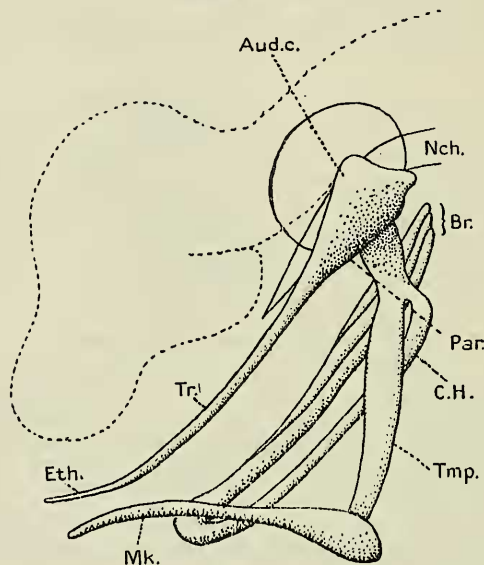
c. Stage 3. The 5.5 mm. larva.

The trabeculae have still further lengthened and are now joined anteriorly in an extensive but very thin ethmoid plate (text-fig. 5) which as yet shows no sign of any of the upgrowths which later form the investment of the olfactory organs. According to Gaupp it has been shown that in *Salmo salar* the cartilage of the ethmoid plate is formed from the epithelium lining the roof of the mouth, and is therefore ectodermal in origin. In *Sebastes* at this stage it can still be seen from the structure of the ethmoid plate that it is formed from a single layer of cells. But a study of the 4.5 mm. stage shows that these cells are derived from a local condensation of connective tissue.

The notochord still reaches well forward and maintains a marked flexure (text-fig. 4). Another peculiarity to be mentioned here is that there is no sign of a fenestra hypophyseos which is normally present in a tropibasic chondrocranium at this stage. The trabeculae are still closely approximated along the whole of their length. The parachordals are now well developed and form broad, saucer-shaped bases to the auditory vesicles.

The visceral skeleton has maintained its advance over the cranial elements. The lower jaw has now attained a considerable length, but there is still no vestige of an upper jaw. In this peculiarity the development resembles that of the larval *Clupea*

Text-figure 4.

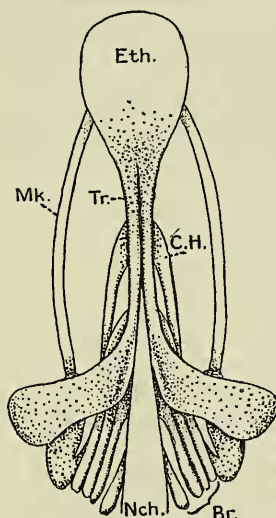


Stage 3. Lateral view of chondrocranium.

(Wells, 1922) in which the upper jaw does not appear until the 13 mm. stage. The temporal cartilage (text-fig. 4) has lengthened, but has otherwise undergone no change except for the fact that the hyomandibular portion is better defined. There is at present no foramen for the hyomandibular branch of the VIIth nerve. It appears that the nerve becomes enclosed in the cartilage later on. The cartilage joining the ceratohyal to the temporal is now constricted to a narrow stylohyal. Considerable development has taken place in the branchial bars (text-fig. 6). There is a median copula communis to which the ceratohyal and the first three branchial bars are attached. The fourth bar is free and the fifth

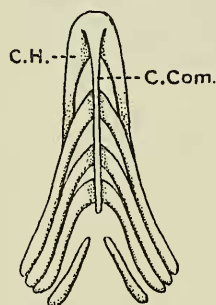
has not yet appeared. The branchial bars occupy a rather advanced position. They form a kind of ridge on the floor of the mouth, the copula communis being at a higher level than the gill-

Text-figure 5.



Stage 3. Dorsal view of chondrocranium.

Text-figure 6.



Stage 3. Dorsal view of branchial bars.

bars which slope downwards and backwards in relation to it. The interior of the mouth is thus in the form of an inverted V when viewed in transverse section.

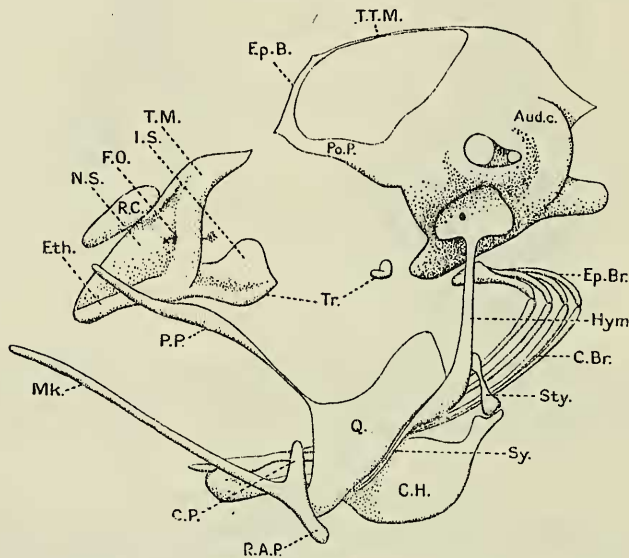
d. *Stage 4. The 25 mm. Stage.*

The chondrocranium may now be looked on as fairly complete (text-figs. 7, 8, and 9). A certain amount of ossification has taken place. As already mentioned I was unable to procure any specimens between this and the 5.5 mm. stage, and at first glance it would seem that the gap is so large that it would be a matter of difficulty to connect the two stages with any profit. However, by a careful study of the complete chondrocranium and by analogy with the changes which take place in other forms, it is possible to reconstruct from a general point of view the processes which bring about the conditions found in the present stage.

The ethmoid region of the mature chondrocranium of *Sebastes* (text-fig. 7) bears a strong resemblance to that of *Salmo*, and there can be little doubt that it arises in much the same manner. In the 25 mm. stage it consists of a substantial mass of cartilage roughly triangular in shape when viewed from the side. The

base of this triangle consists of a thickened plate representing the originally thin ethmoid plate. Above and continuous with this lies the nasal septum which expands posteriorly to form a vertical pillar, the antorbital planum. The upper part of the antorbital planum turns backwards in the form of two lateral horns, the taniæ marginales (text-fig. 8) approaching the extremities of the epiphysial bar and postorbital processes presently to be described. The antorbital planum is pierced on either side by the foramen for the olfactory nerve. The ethmoid structure has evidently arisen from a median ridge and posterior upgrowth on the ethmoid plate, the former giving rise to the nasal septum and the latter to the antorbital planum. It is probable that at a slightly

Text-figure 7.



Stage 4. Lateral view of chondrocranium.

earlier stage the taniæ marginales were connected with the epiphysial bar, and afterwards became separated as is the case in *Gasterosteus* (Swinnerton, 1902). This point will be referred to again later.

The fused trabeculae are now hardly recognisable as such. They are represented by two median pieces of cartilage, one of which is attached to the ethmoid region while the other is a small piece of free cartilage level with the posterior border of the eye. The former remnant of the trabeculae consists of a thickened base resulting from the fusion of the two originally separate elements, bearing a plate-like upgrowth which constitutes an interorbital

septum. This fragmentation of the trabeculae is not uncommon in Teleosts. A somewhat similar process takes place in *Cyclopterus* (Uhlmann, 1921).

Above the nasal septum lies a slightly elongated rostral cartilage. It shows no connection either with the ethmoid or palatine cartilages.

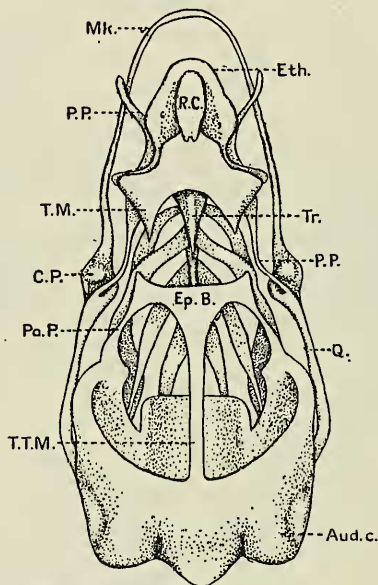
The parachordals have given rise to a substantial investment of the auditory capsules and posterior part of the brain. The notochord has retreated considerably relative to the auditory capsules, and is now bridged over by cartilage. Below and in front of the articulation of the hyomandibular with the auditory capsule a process projects forwards on either side. These probably represent the anterior part of the parachordals. The trigeminal nerve passes out through a notch above them. The auditory capsules are now completely enclosed and the cartilage is continued as a roof over the hinder part of the brain. From the side wall of the brain there runs forward on each side a postorbital process which joins the ends of a transverse bridge, the epiphysial bar. This bar (text-fig. 8) cuts off the posterior dorsal fontanelle, and the fontanelle is divided into lateral halves by a tænia tectum medialis, a thin band of cartilage joining the epiphysial bar with the posterior covering of the cranial cavity. In *Salmo*, *Amia* (Pehrson, 1922), and others the epiphysial bar, being connected also with the tæniæ marginales, forms in addition an anterior dorsal fontanelle which gradually fills up. This anterior roofing in does not occur in *Sebastes*. In *Amiurus* (Kindred, 1919) a permanent anterior fontanelle is formed which, however, does not close up, while in *Gasterosteus* the fontanelle is formed, but the epiphysial cartilage, as is probably the case in *Sebastes*, becomes disconnected from the ethmoid region.

It is now necessary to consider how the cranial elements developed from the parachordals have arisen. It is obvious that there has been a vigorous upward growth from the edges of the cartilage which in the 5.5 mm. stage formed the base of the auditory capsule. This growth has extended so far as to roof over the posterior part of the cranial cavity. The postorbital processes have evidently grown forwards from the lateral walls of the cranium, but it is difficult to say whether the epiphysial bar has arisen independently or whether it has been formed by the joining together of processes growing upward from the ends of the postorbital processes. Independent formation is the more common condition among Teleosts. The tænia tectum medialis is probably a backward growth from the epiphysial bar. This is how it is formed in *Cyclopterus*, and in *Sebastes* the anterior part of the band is broad and strong while the posterior part is very thin and frail.

The changes undergone by the jaw arches and visceral skeleton are almost as great as these displayed by the cranium. The lower jaw is a long, rod-like cartilage bearing coronoid and retro-articular processes at the point of its articulation with the quadrate. In

this respect it resembles the lower jaw of *Amia*. In place of the temporal cartilage we have now the clearly differentiated hyomandibular, symplectic, and quadrate. The hyomandibular presents a rather unusual appearance. It is club-shaped and very long. At its point of articulation with the auditory capsule it has a broad plate-like head which is continued downwards as a comparatively slender stem merging into the symplectic. The latter is also rather longer than usual and runs down close to the lower margin of the quadrate. This is a very large plate of cartilage extended upward and backward as a metapterygoid process. Posteriorly the quadrate is in intimate association with

Text-figure 8.



Stage 4. Dorsal view of chondrocranium.

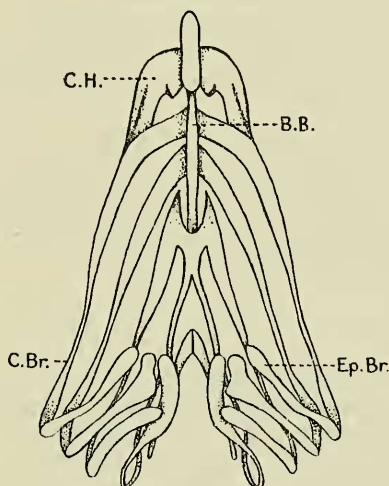
the symplectic but is not continuous with it. The upper jaw, consisting of the palato-ptyergoid cartilage, is now established and runs from the upper anterior angle of the quadrate up to a point level with the anterior end of the rostral cartilage. The posterior end of the palato-ptyergoid is very slender. It passes close to the margin of the ethmoid plate but is not articulated with it. At its extremity it turns outwards (text-fig. 8), reaching almost to the surface of the snout.

The fact that the upper jaw is connected with the quadrate only by a very slender piece of cartilage suggests that it may have arisen independently and grown back to meet the dorso-anterior

angle of the quadrate. This supposition is strengthened by a comparison with the conditions found in the chondrocranium of the larval *Clupea*, in which the upper jaw also arises at a late stage and grows back to join the quadrate in a slender connection. A somewhat similar process occurs in *Amiurus* and *Syngnathus*, in each of which the palatine arises separately.

It appears that the quadrate, symplectic, and hyomandibular have all arisen from the original temporal cartilage. In such a case it might be expected that the three elements were formed separately in the earliest stages, then became fused to form the temporal and finally separated again. In studying the earliest stages in which the temporal can be distinguished I have not been able to trace any division. But in these early stages the

Text-figure 9.



Stage 4. Dorsal view of branchial bars.

cartilage is in an immature condition, and it is very hard always to be certain whether it is continuous or not. It would also be difficult to reconstruct the details of the process by which the differentiation of the hyomandibular, symplectic, and quadrate has come about. It is worth noting that in the 5.5 mm. stage the hyomandibular part of the temporal is very short and that it has become greatly lengthened in the intervening period. The long hyomandibular is a feature correlated with the rather unusual depth of the head in the adult *Sebastes*.

The stylohyal is now a small cartilage articulated with the hyomandibular and ceratohyal. The latter is in the form of a very large plate bearing a posterior process for the articulation with the stylohyal. The anterior part of the ceratohyal tends to

become more rod-like. It is possible that the expansive form of the ceratohyal is correlated with the fact that the gill-bars reach far forward, in that its position suggests that it serves as a protection to the anterior parts of the bars, the posterior parts being of course protected later by the development of the opercular bones. The anterior junction of the ceratohyals is surmounted by a short tongue of cartilage, and there passes back a median bar, the basi-branchial, corresponding to the *copula communis* (text-fig. 9). To this bar are attached the first four branchials. The fifth pair are free but articulate with one another at their bases. The third pair is peculiar in that the base of each is produced forwards in two downwardly directed processes. The ceratobranchials are very long and fairly stout near their articulation with the basibranchial; further back they become very slender, but before meeting the epibranchials they become thicker again. Perhaps the most important development of the branchial elements lies in the appearance of the epibranchials. These are possessed by the first four bars but not by the fifth. They are short in comparison with the ceratobranchials and of a slightly irregular, twisted shape.

Here again it is difficult to fill in any details during the preceding period of development. This, however, is not of great importance as the branchial bars have not undergone any striking changes beyond the addition of the fifth bar, the epibranchials, and a few subsidiary elements.

4. SUMMARY.

1. There is a precocious development of the visceral skeleton.
2. In at least the earlier stages there is no sign of a fenestra hypophyseos.
3. The cranial flexure is retained for a considerable period after hatching.
4. In the 5.5 mm. stage the hyomandibular, symplectic, and quadrate are represented by a simple temporal cartilage. This appears also to be a single piece of cartilage in the earlier stages.
5. The upper jaw does not appear until a comparatively late stage, and there is evidence that it arises independently and grows back to meet the quadrate.
6. The anterior part of the trabeculae gives rise to an interorbital septum of rather limited area.
7. There is a free rostral cartilage situated above the nasal septum.
8. The lower jaw is long and exhibits prominent coronoid and retro-articular processes.
9. The hyomandibular is club-shaped and very long. Its length is correlated with the special depth of the head.

5. ABBREVIATIONS.

Aud.c.	Auditory capsule.	Nch.	Notochord.
B.B.	Basibranchial.	N.S.	Nasal septum.
Br.	Branchial bars.	Par.	Parachordals.
C.Br.	Ceratobranchials.	P.P.	Palato-ptyergoid.
C.Coin.	Copula communis.	Po.P.	Postorbital process.
C.H.	Ceratohyal.	Q.	Quadrate.
C.P.	Coronoid process.	R.A.P.	Retro-articular process.
Ep.B.	Epiphysial bar.	R.C.	Rostral cartilage.
Ep.Br.	Epibranchials.	Sty.	Stylohyal.
Eth.	Ethmoid plate.	Sy.	Symplectic.
F.O.	Olfactory foramen.	Temp.	Temporal.
Hym.	Hyomandibular.	T.M.	Tania marginalis.
I.S.	Interorbital septum.	T.T.M.	Tania tectum medialis.
Mk.	Meckel's cartilage.	Tr.	Trabeculae.

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